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PALYNOLOGICAL UPDATE FROM THE DEVONIAN OF ARGENTINA

The Pescado Formation (Tarija Basin) yielded marine and terrestrial palynomorphs including cryptospores, spores, phytoplankton, and chlorophycean algae.

UPPER PALEOZOIC PALYNOSTRATIGRAPHIC DATA FROM INDIA

The age of the Talchir Formation (Wardha Basin) is revised based on global correlation of palynomorphs.

NEOGENE BONY FISHES FROM NORTHERN CHILE

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AMEGHINIANA - 2021 - Volume 58 (4): 345–368 ARTICLES

NEOGENE BONY FISHES FROM THE BAHÍA INGLESA FORMATION, NORTHERN CHILE

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Abstract. Despite being one of the richest Neogene deposits of marine fossil vertebrates along the Pacific coast of South America, no detailed study of bony fishes from the Bahía Inglesa Formation has been carried out. Through the revision of historical collections of the Caldera Paleontological Museum, we describe 27 fossil remains of bony fishes. Fossils described here are distributed in 13 taxa. Among these, *Sardinops* sp. cf. *S. sagax* (Clupeidae) represents the first fossil record of the genus for Chile, *Labrodon* sp. (Labridae) and *Stelliferinae* (Sciaenidae) are the first respective records for the southeast Pacific Ocean, *Sarda* sp. (Scombridae) represents the first fossil record for South America, *Semicossyphus* sp. (Labridae) and *Anisotremus* sp. (Haemulidae) are the first respective records for the Southern Hemisphere. *Gymnosarda* sp. (Scombridae) is described for the first time for the Neogene. We performed a paleobathymetric analysis of fossil fishes, including elasmobranchs, to understand the paleoenvironment followed by a similarity analysis that compares the faunal composition of the Bahía Inglesa Fm. with other fossil assemblages for the Pacific of South America. Our results show that the fish fauna from the Bahía Inglesa Fm. likely represents a depth range of 98 to 382 m with a mean depth range of 252 m in an uppermost bathyal environment. The assemblage from the Bahía Inglesa Fm. shows low taxonomic similarity levels with other Neogene geological units from the southeast Pacific Ocean. The study represents the first paleoecological and paleobiogeographic analysis of the fossil fish fauna from the Southeast Pacific.

Key words. Atacama region. Clupeiformes. Eastern Pacific. Paleoenviroments. Perciformes. Ophidiiformes.

Resumen. PECES ÓSEOS FÓSILES DE FORMACIÓN BAHÍA INGLESA, NEÓGENO, NORTE DE CHILE. A pesar de ser uno de los depósitos más ricos de fósiles marinos del Neógeno, a lo largo de la costa del Pacífico de América del Sur, no se ha realizado ningún estudio detallado de los peces óseos fósiles de la Formación Bahía Inglesa en Chile. A través de la revisión de las colecciones históricas del Museo Paleontológico Caldera, se describen 27 restos fósiles de peces óseos. Los fósiles descritos aquí están distribuidos en 13 taxa. Entre estos, *Sardinops* sp. cf. *S. sagax* (Clupeidae) representa el primer registro fósil del género en Chile; *Labrodon* sp. (Labridae) y *Stelliferinae* (Sciaenidae) representan los primeros registros para el Pacífico este del Océano Pacifico; *Sarda* sp. (Scombridae) representa el primer registro fósil de América del Sur; *Semicossyphus* sp. (Labridae) y *Anisotremus* sp. (Haemulidae) son los primeros registros para el hemisferio sur, y *Gymnosarda* sp. (Scombridae) es descrito por primera vez para el Neógeno. Se realizó un análisis paleobatimétrico de los peces fósiles, incluyendo elasmobranquios, para entender el paleoambiente, seguido por un análisis de similitud que compara la composición de la fauna de la Fm. Bahía Inglesa con otros ensambles del Pacífico de América del Sur. Los resultados muestran que la ictiofauna de la Fm. Bahía Inglesa es representada probablemente por un rango de profundidad entre 98 y 382 m, con una profundidad media de 252 m en un ambiente batial superior. El ensamble de la Fm. Bahía Inglesa muestra un bajo nivel de similitud taxonómica con otras unidades geológicas del Neógeno en el sudeste del océano Pacifico. Este estudio representa el primer análisis paleoecológico y paleobiogeográfico de la fauna fósil de peces para el Pacifico sudeste.

Palabras clave. Región de Atacama. Clupeiformes. Pacifico este. Paleoambientes. Perciformes. Ophidiiformes.

THE NEOGENE BAHÍA INGLESA FORMATION (Fm.) crops out along the coast of the northern Chilean Pacific coast of South America (27–29° S) and harbors a well-preserved and widely recognized Neogene marine fauna (Le Roux *et al.*, 2016). Paleontological studies have documented the presence of invertebrates (Herm, 1969; Godoy *et al.*, 2003), sharks, rays, bony fishes (Long, 1993; Suárez *et al.*, 2004; Le Roux *et al.*, 2016), reptiles, birds, and mammals (Walsh & Hume, 2001; Walsh

& Naish, 2002; Walsh & Suárez, 2006; Chávez, 2007; Chávez *et al.*, 2007; Canto *et al.*, 2008; Gutstein *et al.*, 2009; Pyenson *et al.*, 2014; Soto-Acuña *et al.*, 2015). Previous studies attempted to understand the fish fauna presenting taxonomic lists (*i.e.*, Suárez *et al.*, 2002, 2010; Suárez & Marquardt, 2003; Gutstein *et al.*, 2008), but only two publications provided detailed descriptions (Long, 1993; Walsh, 2001), of which one is not formally published. The result is that many of the hitherto reported fishes were not illustrated or described in detail, and sometimes it is not possible to confirm the taxonomic identity of the specimens (Suárez *et al.*, 2002, 2010; Suárez & Marquardt, 2003; Gutstein *et al.*, 2008). Here, we aimed at a) analyzing a bony fish collection of the Museo Paleontológico de Caldera, b) reconstructing the paleobiogeographic affinities of the Bahía Inglesa assemblage with other Neogene faunas from the Southeast Pacific, and c) inferring paleoenvironmental conditions, based on the ecological traits of taxa.

Institutional abbreviations. MPC, Museo Paleontológico de Caldera, Caldera, Chile; **STRI,** Smithsonian Tropical Research Institute, Panama City, Panama; **CTPA,** Center of Tropical Paleoecology and Archaeology of STRI, Panama City, Panama; **USNM,** Smithsonian National Museum of Natural History, Washington D.C., USA; **UF,** Florida Museum of Natural History, Gainesville FL, USA; **LACM,** Natural History Museum of Los Angeles Country, Los Angeles CA, USA; **IRSNB,** Institut royal des Sciences naturelles de Belgique, Brussels, Belgium; **MNHN,** Muséum National d'Histoire Naturelle, Paris, France.

Anatomical abbreviations. BO, basioccipital; **BOC,** basioccipital condyle; **D,** dentary; **DR,** dental ridge; **EO,** exoccipital; **EOC,** exoccipital condyle; **EP,** epiotic; **F,** frontal; **HYP,** hypural; **IC,** intercalar; **MX,** maxillar; **P**, parietal; **PF**, prefrontal; **PHP,** parhypurapophysis; **PMX,** premaxillar; **PRO,** prootic; **PS,** parasphenoid; **PTO,** Pterotic; **PTS,** pterosphenoid; **SO,** supraoccipital; **SOR,** supraoccipital ridge; **T,** teeth; **TG,** temporal grove; **UN,** uroneural; **V,** vertebra.

GEOLOGICAL SETTING

The Bahía Inglesa Fm. belongs to the Caldera Basin and is composed of nine members of coastal marine origin ranging from the middle Miocene (15.3 Ma) to early Pleistocene (2.4 Ma) (Le Roux *et al.*, 2016). It is located within the northern section of the flat subduction of the Juan Fernandez Ridge (**JFR**) under the South American plate (Pardo *et al.*, 2002; Achurra *et al.*, 2009). The Bahía Inglesa Fm. includes some of the most diverse fossiliferous deposits in the Neogene of Chile and is one of the best-preserved fossil vertebrate sites in the world (Mayr & Rubilar-Rogers, 2010; Pyenson *et al.*, 2014; Villafaña *et al.*, 2019). Two localities from the Bahía Inglesa Fm. are studied here: Mina Fosforita and Norte Bahía Caldera (Walsh & Hume, 2001; Le Roux *et al.*, 2016; Valenzuela-Toro *et al.*, 2016). Mina Fosforita is one of the best-known vertebrate-bearing areas within the Bahía Inglesa Fm. and is composed of large outcrops of a phosphatic bonebed (Godoy *et al.*, 2003). The Norte Bahía Caldera fossil site is located ~2 km West of Cerro Ballena and ~4 km North of the town of Caldera (Valenzuela-Toro *et al.*, 2016). Norte Bahía Caldera stratigraphically corresponds to the Lechero Member (Canto *et al.*, 2008), which was named by Walsh & Suárez (2006) and also to the stratigraphic unit 3 of Walsh & Hume (2001). The Lechero Member is composed of sand and siltstone (Canto *et al.*, 2008) and contains remains of the aquatic sloth *Thalassocnus*, arbitrarily assigned to *T. natans* based on the presence of this species in Cerro Ballena Member (Pyenson *et al.*, 2014). The presence of this aquatic sloth is an indicator of a late Miocene age in the Pisco Fm. (de Muizon & DeVries, 1985). K-Ar dating 7 m above the top of the underlying phosphatic bonebed suggests an age of ~7.6 Ma for Norte Bahía Caldera (Marquardt, 1999). A recent stratigraphic revision of the Bahía Inglesa Fm. does not recognize the sandstones and siltstones of Lechero as an independent Member (Le Roux *et al.*, 2016), and unit 3 North of Bahía Caldera of Walsh and Hume (2001) is included within the Mina Fosforita Member, which has an age of ~7.0 Ma (Le Roux *et al.*, 2016). Both localities studied belongs to the Mina Fosforita Member, which is a generally fining-upward, reddish-brown succession of medium to fine-grained sandstones, siltstones, and shales, with at least one fossil-rich, nodular phosphate bed and manganese nodules in its basal portion (Carreño, 2012; Le Roux *et al.*, 2016).

MATERIALS AND METHODS

Fossil Material

Here, we analyze 27 fossil remains of bony fishes, including dentaries, crania, pharyngeal tooth plates, opercular bones, and rostra. The material forms part of the historical

collections from two fossiliferous localities (Mina Fosforita and Norte Bahía Caldera) housed in the Museo Paleontológico de Caldera, Atacama, Chile with the prefix MPC. Although the information regarding the specific collection sites is missing for some specimens (MPC-456, -457, -458, -459, -460, -461, -462, -463, -465, -467), some of them are assigned to Mina Fosforita and others to Norte Bahía Caldera based on the type of preservation and associated lithology of the rock matrix, respectively (Fig. 1).

Statistical analysis

An analysis of the relative abundance of the fish fauna of the Bahía Inglesa Fm. was carried out using newly identified and previously published taxa. We performed a paleobathymetric analysis following Nolf and Brzobohaty (1994) methodology for fossil bony fishes and sharks (Carrillo-Briceño *et al.*, 2015, 2016a, 2016b, 2020). Cross-validation, employing a second paleobathymetric analysis, was conducted following the methodology of Pérez *et al.* (2017)

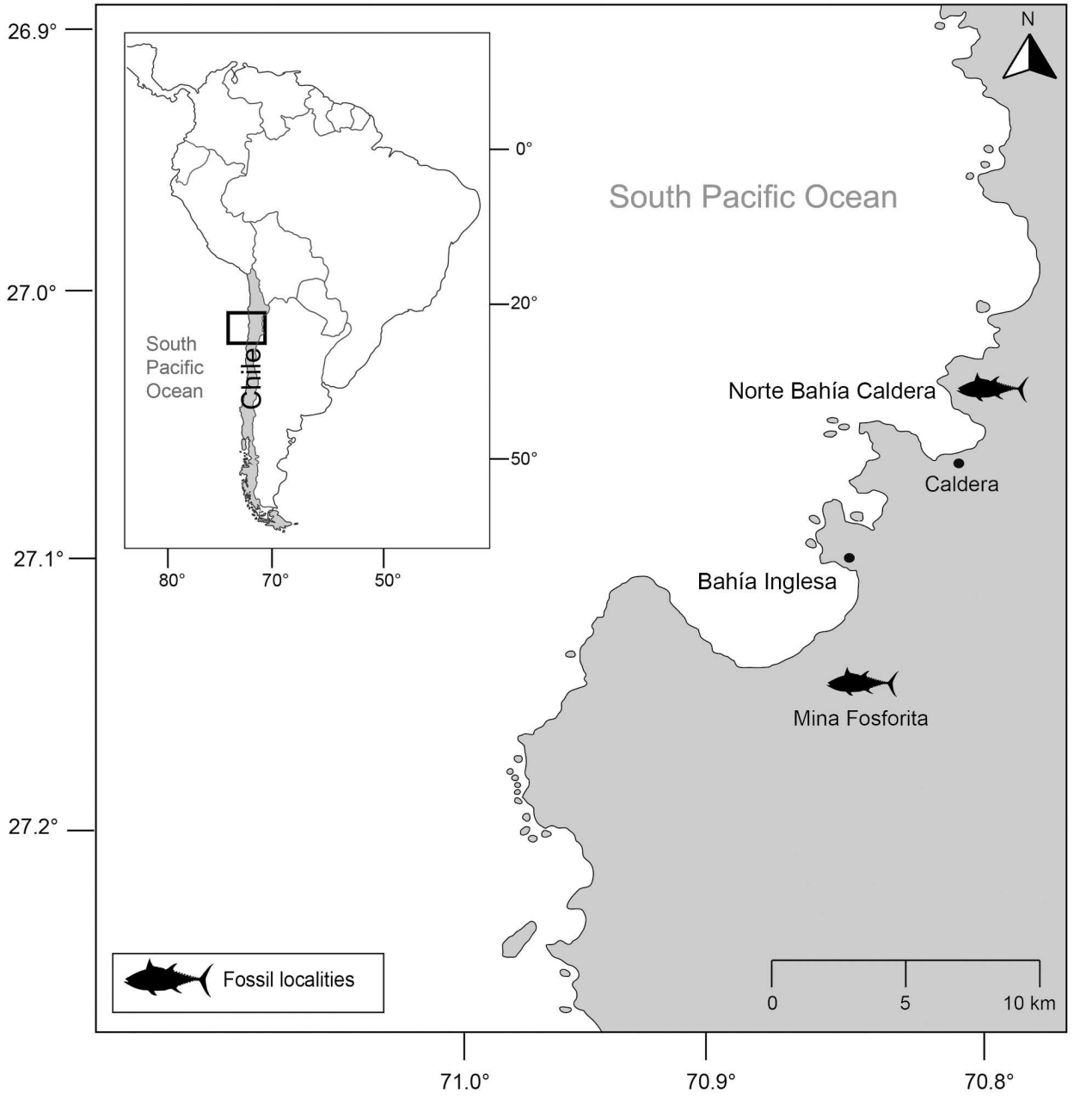

Figure 1. Map showing the fossiliferous localities referred to in this study.

using R (R Development Core Team, 2020). This paleobathymetric estimator uses weighted bootstrap to estimate the depth distribution of the sampled population and its parameters as outlined in Carrillo-Briceño *et al.* (2020). The statistic estimator was the difference between the minimum and maximum mean depth range, and the weight estimator used was the number of individuals. The data set was resampled 10,000 times and plotted as a histogram that provides the mean depth and the 95% confidence interval using a percentile method. The raw data and the script for paleobathymetric analysis are included in Data S1. For both analyses, we included only species/ genera with closely related extant taxa. Extinct taxa without clear living representatives were removed. Our analysis includes a total of 53 (out of 64) taxa that represent a total of 808 individuals for which ecological information is available.

We also compared the taxonomic composition of the fish fauna from the Bahía Inglesa Fm. with other geological formations along the eastern Pacific of South America to study the geographic relationships of these assemblages using the Sorensen-Dice similarity index, which is highly recommended in previous ecological and paleontological studies due to its statistical properties (Murguía & Villaseñor, 2003; Hammer & Harper, 2006; Villafaña *et al.*, 2020).

Comparative Materials

The following extant specimens were used for fossil comparisons: Clupeidae: *Sardinops sagax* (Jenyns, 1842), MNHN-5036. Labridae: *Bodianus diplotaenia* (Gill, 1862), dentaries MNHN-6689 and MNHN-6689; *Cheilinus lunulatus* (Forsskål & Niebuhr, 1775), dentary MNHN-ICOS-00256; *Semicossyphus maculatus* (Jenyns, 1842), dentary in Falabella *et al.* (1995, fig.14a), pharyngeal jaw and infrabranchial bone in Falabella *et al.* (1995, fig. 42c.1). Sciaenidae: *Argyrosomus regius* (Asso, 1801), maxilla MNHN-A-5; *Cilus gilberti* (Abbott, 1899), maxilla MNHN-4005; *Cynoscion albus* (Günther, 1864), maxilla MNHN-6681; *Paralonchurus peruanus* (Steindachner, 1875), maxilla MNHN-5173; *Sciaena deliciosa* (Tschudi, 1846), maxilla MNHN-5048; *Pomadasys panamensis* (Steindachner, 1875), maxilla MNHN-8043; *Anisotremus scapularis* (Tschudi, 1846), maxilla MNHN-5165. The skulls of the first five species mentioned above were also studied. Centropomidae: *Centropomus unionensis* (Bocourt, 1868), cranium MNHN-6795. Ophidiidae: *Genypterus maculatus* (Tschudi, 1846), cranium MNHN-5232. Scombridae: *Euthynnus lineatus* Kishinouye, 1920, dentary MNHN-6663; *Scomber japonicus* Houttuyn, 1782, dentary MNHN-5013; *Thunnus albacares* (Bonnaterre, 1788), dentary MNHN-ICOS-00491; caudal complex of the family Scombridae (Collette, 1978, fig. 2). *Merluccius gayi* Guichenot, 1848 (MNHN-5124); *Genypterus maculatus* (Tschudi, 1846) (MNHN-5232). Xiphiidae: *Xiphias gladius* Linnaeus, 1758 (Swordfish): USNM 110042 entire skeleton. Istiophoridae: *Istiophorus platypterus* (Shaw, 1792) (sailfish): STRI archeology collection 1628 entire skeleton, MNHN A-9463 skull, MNHN A-9464 skull, MNHN 6960 complete skeleton; *Makaira nigricans* Lacépède, 1802 (blue marlin): USNM 196019 entire skeleton, LACM 46023-1 vertebral column, MNHN 1892-1050 rostrum; *Istiompax indica* (Cuvier, 1832) (black marlin): LACM 25509 entire skeleton, UF 210017 pectoral girdle, MNHN 1884.29 pectoral fin, MNHN A-5514 rostrum fragment, MNHN 2003-0420 complete dry specimen; *Kajikia albida* (Poey, 1860) (white marlin): USNM 270766 skeleton, USNM 3605507 axial skeleton; *Kajikia audax* (Philippi, 1887) (striped marlin): USNM 372777 entire skeleton, MNHN 6821 entire skeleton, LACM 25500 skull; *Tetrapturus pfluegeri* Robins & de Sylva, 1960 (long bill spearfish): LACM 25462 entire skeleton, UF 208789 vertebral column and pectoral fin girdle; *Tetrapturus belone* Rafinesque, 1810: MNHN A-7504 entire skeleton; *Tetrapturus angustirostris* Tanaka, 1915 (short bill spearfish): LACM 25499 entire skeleton. The fossil specimens also were compared to images of actinopterygian bones provided by an online collection database of the National Museum of Natural History Paris, France (Tercerie *et al.*, 2016).

Osteological Nomenclature and measurements

We employed the traditional terminology for skull roofing bones, which is “frontal” instead of “parietal” and “parietal” instead of “postparietal.” Consequently, the osteological terminology of fossils follows a combination of that proposed by Jollie (1986), Rojo (1988), Sasaki (1989), Falabella *et al.* (1995), and Boyle (1997). We used taxonomical and osteological information for the classification of fossil Clupeidae from Ridewood (1904), Phillips (1942), and Grande (1985). We followed Toro & Dazarola (1965) and Nielsen *et al.* (1999) for the morphology and classification of Ophidiidae. For Istiophoridae, we used the method of Fierstine and Voigt (1996), Fierstine (1998), and Fierstine

et al. (2001) for billfish classification using rostral traits. We employed the comparative morphology of Collette and Chao (1975), and we followed Monsch (2000, 2006) and Monsch and Bannikov (2011) for the description of fossil Scombridae. For fossil remains of Labridae and Haemulidae we used osteological information from Rosen and Patterson (1990) and Gomon (1995). For Sciaenidae we used the comparative morphology and classification method of Sasaki (1989). Linear measures of bones were made to the nearest 0.5 mm with dial calipers or a measuring tape, and we followed the systematics of Nelson *et al.* (2016) for the general classification scheme of the fossils presented here.

SYSTEMATIC PALEONTOLOGY

Order CLUPEIFORMES Bleeker, 1859
Suborder CLUPEOIDEI Bleeker, 1859
Family CLUPEIDAE Bleeker, 1859
Subfamily CLUPEINAE Gill, 1861

Genus ***Sardinops*** Hubbs, 1929

Type species. *Clupea sagax* Jenyns, 1842: 134.

Sardinops sp. cf. ***S. sagax***
Figure 2.1–2.8

Referred material. Six skulls (MPC-90, -91, -462, -463, -748, and -753) and one operculum (MPC-27).

Geographic occurrence. Mina Fosforita and Norte Bahía Caldera, Chile.

Description. The cranium is moderately elongated and wedge-shaped, and the parietal bones are completely separated by the supraoccipital. The skulls of the specimens described here do not preserve the vomer, which is placed at the distal end of the cranium. The preserved crania in all specimens described here range from 32 to 69 mm in length (MPC-90: 55 x 30 x 15 mm; MPC-91: 69 x 30 x 15 mm; MPC-462: 37 x 28 x 14 mm; MPC-463: 32 x 22 x 13 mm; and MPC-748: 38 x 31 x 16 mm). In all specimens, the frontals are the largest bones, which display various groves. Anteriorly, the internal sides of one grove form a pair of longitudinal ridges. The frontals meet anteriorly along an M-like suture. The medial parts of both frontals are depressed, forming a long, wide, and shallow channel on the dorsal surface of the cranium. There is a small transverse hump in the medial section of the suture of both frontals, which are aligned back to the front edges of the sphenotic processes. The parietal groves are at the upper surface of the pterotic. These groves extend from posterolateral portion of the backward frontal past the parietal and out between the epiotic and the pterotic. A large temporal foramen opens in the cranium at the anterior end of the temporal groves. The epiotic bones are posteriorly elongated and fused basally with the supraoccipital and parietal bones. In dorsal view, these bones are forming a crest that is projected backward. Both crests are projected, forming an angle of about 45° from the central axis of the cranium. In ventral view (Fig. 2.7), the parasphenoid bone starts in the ethmoidal region extending to the basioccipital bone, which underlies the exoccipital region. The alveolar process is filled with a matrix and thus cannot be properly observed. The only preserved opercular bone MPC-27 (40 x 41 x 0.7 mm; Fig. 2.8) is rather flat with 10 regular grooves on its proximal edge, giving it a fan-shaped appearance. The isolated operculum is highly diagnostic by having groves present on the lateral side that radiates from the antero-dorsal margin (Casteel, 1975).

Remarks. These crania assigned to *Sardinops* are moderately elongate and somewhat wedge-shaped, with a subepidotic fossa, hyomandibular embrasure on the upper inner face of the hyomandibular, and evidence of a filamentiferous rod where a branched bone in the nape region is attached. These crania are identical to *Sardinops sagax* and only differ in the angle formed by the projection of the epiotics, which is more acute, while in *S. sagax* it is more rounded. The anterior projection of the supraoccipital also is larger, and the transverse hump is aligned posteriorly to the pterotics. Therefore, we assign these skulls to *Sardinops* sp. cf. *S. sagax*, by displaying these differences, and a more detailed study of these specimens should be done to establish whether they belong to this species or represent a different taxon. The South American pilchard *S. sagax*, is the only extant representative of the genus and occurs in the Indo-Pacific and Eastern Pacific (Froese & Pauly, 2020), but other species are known from the fossil record (*e.g.*, Burdigalian of New Zealand; Schwarzhans, 2019). The fossil record of *S. sagax* is scarce, with some reports from the Pleistocene of

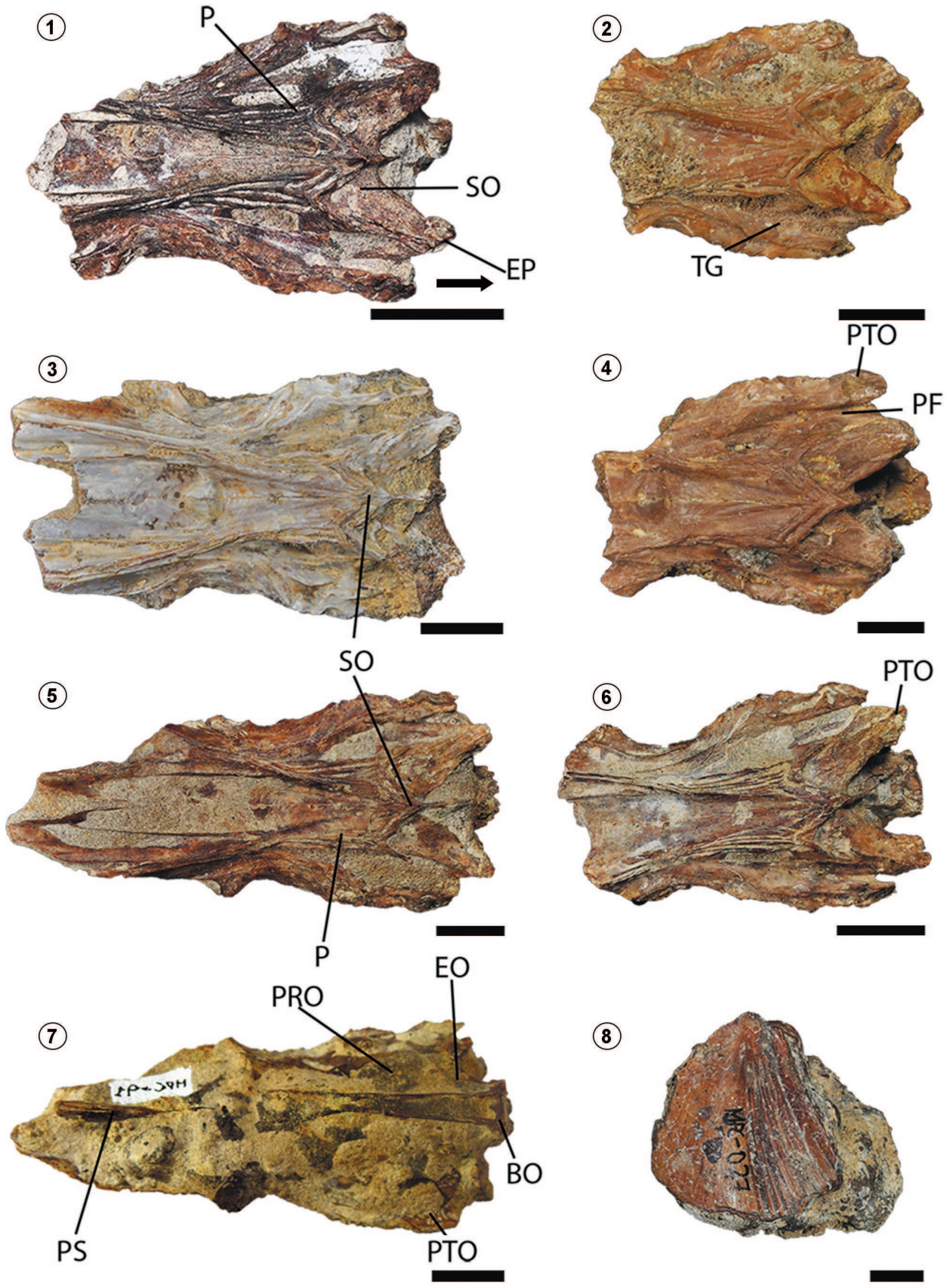

Figure 2. 1–8, ***Sardinops*** sp. cf. ***S. sagax***, MPC-463, 462, 748, 753, 91, 90, 27; **1–3, 5–7,** dorsal view of crania; **4,** ventral view of the cranium; **8,** opercular bone, external view. Scale bar equals 1 cm.

the United States (Long, 1993) and the late Miocene of Peru (Collareta *et al.*, 2015; Lambert *et al.*, 2015). The specimens described here represent the first fossil record of this taxon in Chile.

Order OPHIDIIFORMES sensu Cohen & Nielsen, 1978
Family OPHIDIIDAE Rafinesque, 1810
Subfamily OPHIDIINAE Rafinesque, 1810
Tribe LEPOPHIDIINI Robins, 1961

Genus ***Genypterus*** Philippi, 1857

Type species. *Conger chilensis* Guichenot, 1848 (= *Genypterus nigricans* Philippi, 1857: 185–186).

Genypterus sp.
Figure 3.1–3.2

Referred material. Two nearly complete skulls (MPC-33 and-208).

Geographic occurrence. Mina Fosforita, Chile.

Description. Both skulls are rectangular, elongated, and slightly dorso-ventrally fattened. Specimen MPC-33 measures 92 mm in length and 32 mm in width (Fig. 3.1), whereas specimen MPC-208 measures 117 mm in length and 40 mm in width (Fig. 3.2). In dorsal view, the sphenotics contact the external border of the frontals at about the middle of the cranium. The frontals are the longest preserved bones, and they are at least two and a half times longer than the parietals. The parietals are elongated and slender and are in contact posteriorly with the frontals. Laterally the parietals are enclosed by the pterotics and anterolaterally by the epiotics. Both parietals are separated by the supraoccipital, which is the impar bone placed centrally at the anterior end of the skull in dorsal view (Fig. 3.1–3.2).

Remarks. MPC-33 and 208 are assigned to *Genypterus* based on the elongated and rectangular shape in dorsal view, and being dorso-ventrally depressed, with a postorbital length of the head at least twice the length of the anterior skull, including the orbit (in the fossil expressed as the distance from the anterior outline to the orbit aperture) (Toro & Dazarola, 1965; Nielsen *et al.*, 1999).

Genypterus is represented by six extant species (*G. blacodes*, *G. brasiliensis*, *G. capensis*, *G. chilensis*, *G. maculatus*, and *G. tigerinus*). Adults are common on the rocky bottom of the continental shelf, while juveniles inhabit shallower waters (Nielsen *et al.*, 1999; Froese & Pauly 2020). The fossil record of *Genypterus* is known from the Oligocene and Plio-Pleistocene of New Zealand (Schwarzhans, 1980; Nolf & Steurbaut, 1989), Neogene of Ecuador (Aguilera *et al.*, 2011), and Miocene of Argentina (Rossi *et al.*, 2001). In Chile, this taxon was previously reported from the late Pliocene Horcón Fm. (Carrillo-Briceño, 2011). The skulls described here confirm the presence of *Genypterus* in the Miocene of Chile.

Order ISTIOPHORIFORMES Betancur-R. *et al.*, 2013
Family ISTIOPHORIDAE Robins & de Sylva, 1960

Genus ***Makaira*** Lacépède, 1802

Type species. *Makaira nigricans* Lacépède, 1802.

Makaira sp.
Figure 3.3–3.4

Referred material. Two partially preserved rostra (MPC-30 and MPC-31).

Geographic occurrence. Mina Fosforita, Caldera, Chile.

Description. Specimens MPC-30 and MPC-31 are large, stout, and massive rostra formed by the fusion of premaxillaries, maxillaries, and prenasals. One of the rostra (MPC-30) is broken proximally and measures 393 mm in length, 40 mm in width, and 28 mm in height (Fig. 3.3). The distal tip is pointed and covered with alveoli that indicate the position of the denticles (Fig. 3.3). In dorsal view, it has two longitudinal groves that represent the space where the prenasals originally were placed (Fig. 3.3).

The specimen MPC-31 (Fig. 3.4) is a proximal section of a rostrum measuring 268 mm in length, 59 mm in width, and 32 mm in height, preserving the prenasals, which are attached dorsally. In ventral view, it is densely covered by small denticles. Basally, the distal ends of broken maxillaries are attached to the rostral fragment (Fig. 3.4).

In both MPC-30, and MPC 31, the remaining parts represent half of the total length (0.5 L distance). In cross-section, both are oval and dorso-ventrally compressed with two internal longitudinal canals.

Remarks. MPC-30 and MPC 31 are assigned to *Makaira* due to having a large-sized, stout, and massive rostrum and

because the preserved anterior part of the rostrum in dorsal view has an outline formed by the premaxillaries. *Makaira* is a genus, represented by one worldwide-distributed oceanic species (*M. nigricans*), inhabiting tropical to subtropical areas (Nakamura, 1983, 1985). Fossil specimens are known from the late Miocene–Pliocene of the Mediterranean Sea, North America, and Central America (Fierstine, 2006). The presence of *Makaira* sp. in Bahía Inglesa Fm. represents the southern-most fossil record of the genus, as well as for the family Istiophoridae (Gutstein *et al.*, 2008; this work).

Istiophoridae gen. *et* sp. indeterminate

Figure 3.5–3.7

Referred material. Articulated vertebrae representing the

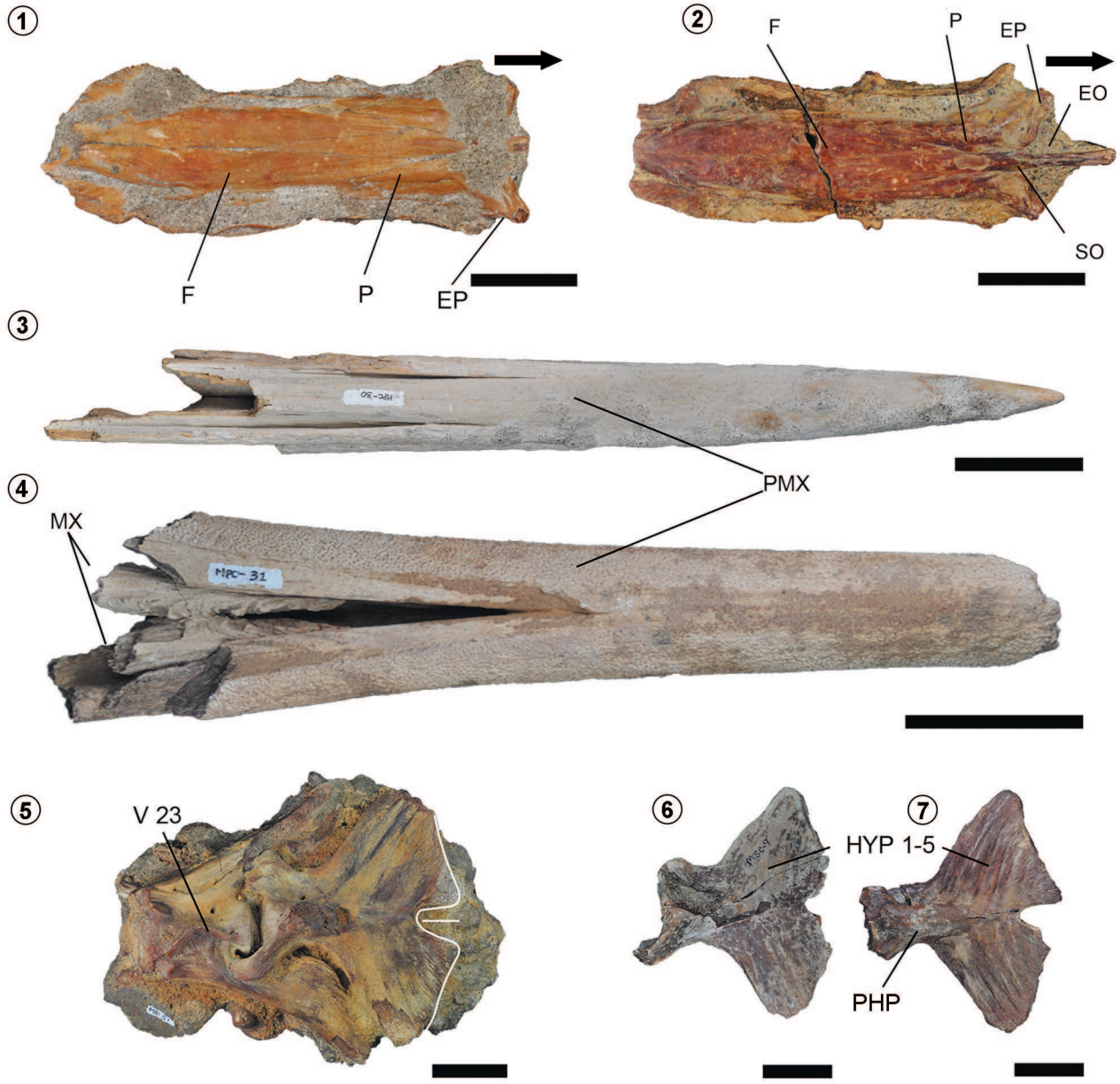

Figure 3. 1–2, *Genypterus* sp., MPC-33, 208; **1–2,** dorsal view of crania, arrow indicating anterior. **3–4, *Makaira*** sp., MPC-30, 31; **3,** distal fragment of rostrum, ventral view; **4,** proximal fragment of rostrum, ventral view. **5–7,** Istiophoridae indeterminate, MPC-51, 193, 194; **5,** Articulated vertebrae no. 23 and 24; **6-7,** two isolated vertebrae no. 24. Scale bar equals **1–2,** 2 cm; **3–4,** 5 cm; **5–7,** 3 cm.

23rd and 24th vertebra (MPC-51) and two isolated vertebrae of the 24th position (MPC-193 and 194).

Geographic occurrence. Mina Fosforita, Chile.

Description. The following description is based on specimen MPC-51 representing the last two caudal vertebrae, which are articulated (Fig. 3.5). Vertebra no. 23 is unusually short compared to vertebra no. 24, which forms the hypural plate. Vertebra no. 23 has a centrum length (**CL**) of 53 mm. The length from the anterior edge of the centrum to the anterior margin to the spinal foramen (**AS**) is 35.72 mm, and the length from the posterior edge of the centrum to the posterior margin of the spinal foramen (**PS**) measures 16.97 mm. The hypural plate (vertebra 24) is nearly complete, only the left hypurapophysis is broken, and the dorsal and ventral tips of the hypural plate are partially broken. The length from the anterior edge of the centrum to the hypural notch (**HL**) is 72.82 mm, the length of the hypural notch (**HNL**) is 21.71 mm, and the length from the dorsal tip of the hypural plate to the ventral tip (**HH**) is 133.37 mm.

Remarks. These vertebrae are assigned to Istiophoridae by being characterized by a triangular hypural plate formed by three fussed epurals, uroneural and parahypural, and by possessing a deep posterior notch between the lower and upper hypural plates. We assigned specimens MPC-51, -193, and -194 to Istiophoridae gen. *et* sp. indet., by having an unusually short vertebra no. 23, if compared to the hypural plate. A proportionally shorter vertebra no. 23 is a trait that is not observed in any living istiophorids (De Gracia, pers. observ.). Despite its striking morphology, we nevertheless refrain from assigning it to a new species because the taxonomy of extinct istiophorids is based on rostra an there are not known articulated fossil specimens with postcranial elements as caudal vertebrae.

The 11 extant istiophorid species inhabit tropical and subtropical waters of all oceans and seas (Fierstine, 1978, 1990; Nakamura, 1985). Istiophorids are pelagic fishes usually found in surface water layers up to 200 m depth (Nakamura, 1983; Froese & Pauly, 2020). They are active and voracious predators, using their long rostrum to capture prey, feeding mainly on cephalopods, sardines and anchovies (Clupeidae), tunas (Scombridae), and mackerels (Carangidae) (Nakamura, 1983, 1985). Istiophorids can reach body lengths of 400 cm and a ton of weight depending on the species (Nakamura, 1983; Nelson, 2006).

Order SCOMBRIFORMES Bleeker, 1859

Scombriformes gen. *et* sp. indeterminate

Figure 4.1–4.2

Referred material. A single middle section of a right dentary (MPC-467).

Geographic occurrence. Mina Fosforita, Chile.

Description. MPC-467 measures 55 mm in length, 9 mm in width, and 13 mm in height (Fig. 4.1–4.2). This dentary fragment is very elongated and proportionally low, with an imperceptible curvature. The teeth are large, pointed, and caniniform in shape. They are solidly fixed in tooth sockets and arranged pairwise along the dentary margin.

Remarks. The middle section of the dentary is straight without any visible curvature, similar to that of extant *Scomberomorus* species (Scombridae). However, the canine teeth separated into groups of two are not observed in *Scomberomorus*. For this reason, we assign the specimen as undetermined Scombriformes due to the high levels of uncertainty because of poor preservation.

Suborder SCOMBROIDEI Bleeker, 1859

Family SCOMBRIDAE Rafinesque, 1815

Tribe SARDINI Jordan & Evermann, 1896

Genus ***Sarda*** Cuvier, 1829

Type species. *Scomber sarda* Bloch, 1793.

Sarda sp.

Figure 4.3

Referred material. An isolated hypural plate (MPC-465).

Geographic occurrence. Mina Fosforita, Chile.

Description. Specimen MPC-465 is a triangular hypural plate, which is composed of five fused hypural bones. Hypural bone 5 is not completely fused and is identifiable by a long fracture dorsally (Fig. 4.3). The plate lacks a caudal notch. The posterior margin is sinuous with a central convexity, being small with 28 mm in length and 45 mm in height. Ventrally, a concave parhypurapophysis is present, where it articulates with the parahypural.

Remarks. MPC-465 is assigned to *Sarda* sp. because the hypural bone 5 is not completely fused to the hypural

plate and because it lacks a caudal notch, having a sinuous posterior margin, and presence of parhypurapophysis. The genus *Sarda* is currently represented by five species (*S. australis*, *S. chilensis*, *S. lineolata*, *S. orientalis*, and *S. sarda*) with a worldwide distribution (Froese & Pauly, 2020). The fossil record of *Sarda* extends back into the Eocene (Snetkov, 2011). Neogene record includes Asia (Popov *et al.*, 2008), Africa (Gaudant, 2008), Europe (Landini & Sorbini, 1992), and North America (Purdy *et al.*, 2001). MPC-465 represents the first fossil record of *Sarda* from South America.

Genus ***Gymnosarda*** Gill, 1862

Type species. *Thynnus unicolor* Rüppell, 1835.

Gymnosarda sp.

Figure 4.4

Referred material. A single isolated hypural plate (MPC-196).

Geographic occurrence. Mina Fosforita, Chile.

Description. MPC-196 corresponds to an isolated hypural

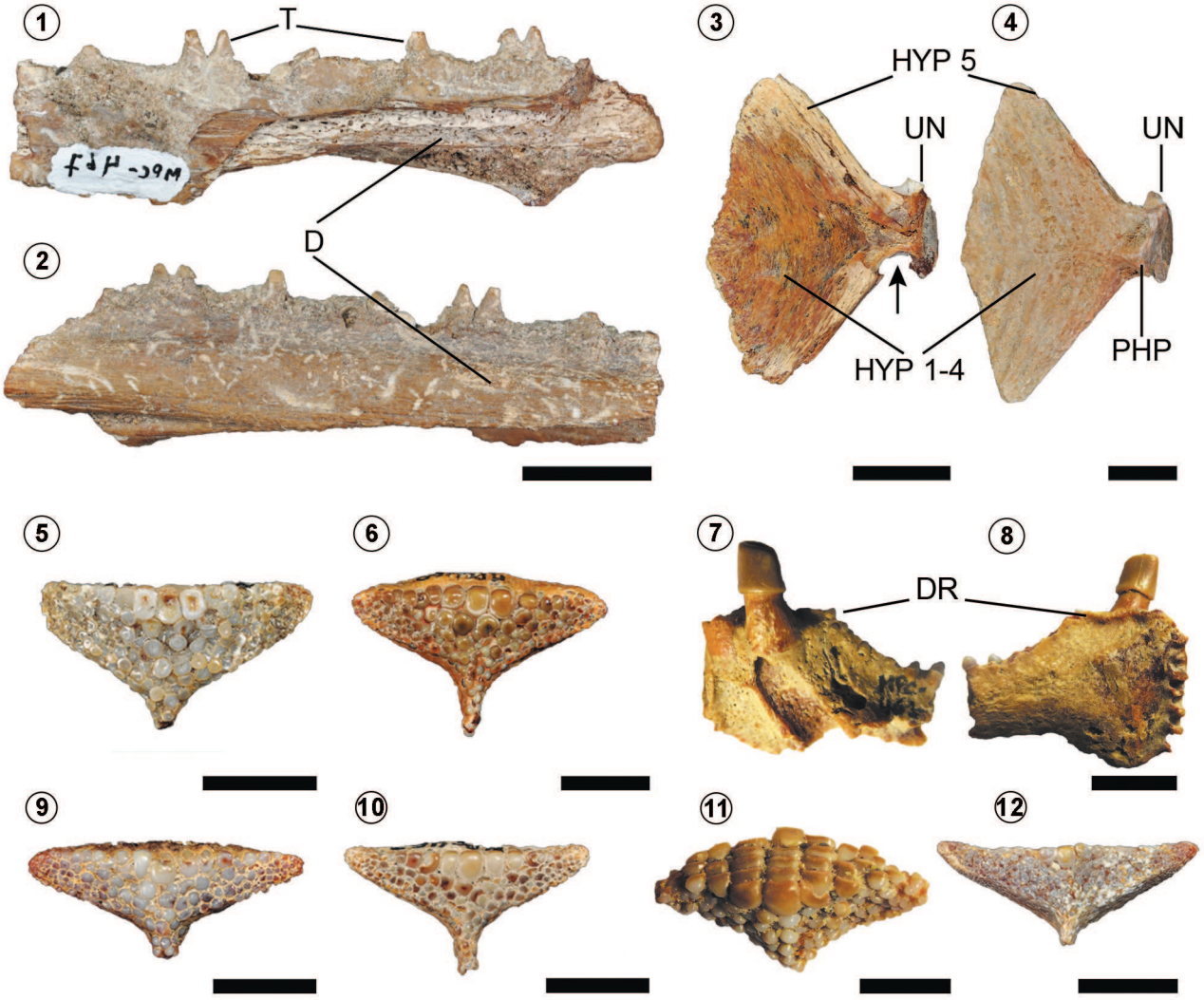

Figure 4. 1–2, Scombriformes gen. *et* sp. indeterminate, MPC-467; **1–2,** a single middle section of a right dentary. **3, *Sarda*** sp., MPC-465; one hypural plate. **4, *Gymosarda*** sp., MPC-196; one hypural plate. **5–6, *Labrodon*** sp., MPC-460, 458; two teeth batteries of the lower pharyngeal jaws. **7–8, *Semicossyphus*** sp., MPC-461; one left dentary with two associated canine teeth. **9–12,** Labridae gen. *et* sp. indeterminate, MPC-459, 457, 627, 456; four lower pharyngeal jaw teeth battery. Scale bar equals 1 cm.

plate, which measures 23 mm in length and 32 mm in height. It is rhomboid in outline, formed by the fusion of five hypurals, of which hypural 5 is not completely fused, being broken with a small fracture dorsally. The posterior process of the hypural plate is single and large. The parahypural is fused with the hypural plate ventrally, and the caudal notch is absent (Fig. 4.4).

Remarks. MPC-196 is assigned to *Gymnosarda* because the hypural bone 5 is not completely fused at its distal tip, the caudal notch is absent, it has a rhomboid shape, and a parahypural that is fused with the hypural plate ventrally. *Gymnosarda unicolor* is the only extant member of this genus inhabiting the Indo-Pacific Ocean (Froese & Pauly, 2020). The oldest fossil record of *Gymnosarda* was reported from the Eocene of the United Kingdom (Monsch & Bannikov, 2011) and the United States (Ebersole *et al.*, 2019). Remains of *Gymnosarda* were also described from the Oligocene of Hungary (Hegedus, 1959) and Romania (Pauca & Ciobanu, 1978). MPC-196 represents the first unambiguous fossil record of *Gymnosarda* from the Neogene.

Order LABRIFORMES Nelson *et al.*, 2016
Family LABRIDAE Cuvier, 1816

Genus ***Labrodon*** Gervais, 1857

Type species. †*Labrodon pavimentatum* Gervais, 1857.

Labrodon sp.
Figure 4.5–4.6, 4.9–4.10

Referred material. Four tooth batteries of the lower pharyngeal dentition (MPC-457, -460, -458, and -459).

Geographic occurrence. Mina Fosforita and Norte Bahía Caldera, Chile.

Description. The lower pharyngeal jaw is triangular in outline, densely covered by molariform-like teeth, which have rounded borders and vary in shape and size. Posteromedial molars are larger, oval to trapezoid in outline, and globular. Teeth are placed close to the margins and anteriorly are much smaller, tending to be elongated and oval in shape.

Remarks. The description of the specimens presented here coincides with the diagnosis for *Labrodon* (Gervais, 1857; Betancourt Lozano, 2012). Fossil remains *Labrodon* are very common in Neogene deposits of Europe and Africa (Pickford & Senut, 1997; Bellwood *et al.*, 2019). In the Americas, this genus was reported from the Miocene of Costa Rica (Laurito *et al.*, 2014) and the early Miocene of Argentina (Cione, 2002). The Caldera specimens represent the first fossil record of *Labrodon* from the eastern Pacific of South America.

Genus ***Semicossyphus*** Ayres, 1854

Type species. *Cossyphus reticulatus* Valenciennes, 1839 (in Cuvier & Valenciennes, 1839: 139).

Semicossyphus sp.
Figure 4.7–4.8

Referred material. One left dentary with two associated, abraded canine-like teeth (MPC-461).

Geographic occurrence. Norte Bahía Caldera, Chile.

Description. MPC-461 preserves only its anterior portion, where two prominent anterior canine-like teeth are located. The first one is slightly smaller than the second one, but only its base is preserved. These teeth are located on the anterolateral side of the dental ridge, with the anterior one being situated more mesially, while the second one is more dorsally and slightly laterally placed. There are no teeth anterior to the dental ridge. Posterior to the canine-like teeth, a row of small teeth or alveoli is present on the crest of the dental ridge (Fig. 4.6–4.7). Teeth located anteriorly in the row are slightly longer than the posterior teeth. The canine-like teeth are large, massive, and slightly curved inward. The root is conical, being considerably thickened at the base, and the crown thickness overcomes the upper part of the root (Fig. 4.7–4.8).

Remarks. MPC-461 is assigned to *Semicossyphus* because of the two prominent and accentuated anterior canine-like teeth (in the present specimen, they are worn) that are very pointed and located anterolateral to the dental ridge, lack of teeth anterior to the dorsal ridge, and the short row of small teeth on the crest. The genus *Semicossyphus* is currently represented by three extant species distributed in the eastern and western Pacific Ocean (Froese & Pauly, 2020). Fossils of *Semicossyphus* were reported from the Neogene (Barnes *et al.*, 1981) and Quaternary of the United States (Langenwalter, 1975). The specimen reported here from

Caldera represents the first fossil record of *Semicossyphus* from the Southern Hemisphere.

Labridae gen. *et* sp. indeterminate
Figure 4.11–4.12

Referred material. Two lower pharyngeal tooth batteries (MPC-456 and -627).

Geographic occurrence. Mina Fosforita and Norte Bahía Caldera, Chile.

Description. MPC-627 (morphotype 1) is a triangular lower pharyngeal tooth plate that displays a convex posterior margin in the dorsal view (Fig. 4.11). It is covered densely with rounded molariform-like teeth that vary in shape and size. In dorsal view, the anterior margins are concave and delimited by a series of four aligned teeth. The posteromedial molars are larger, globular, and trapezoid to rectangular, overlapping each other. Teeth placed close to the margins and anteriorly are smaller and tend to be squared to subcircular.

Specimen MPC-456 (morphotype 2) differs from MPC-627 in being a pharyngeal tooth plate characterized by a triangular shape with a slightly convex posterior margin in dorsal view (Fig. 4.12). MPC-627 is also densely covered with small molariform-like teeth, which are mostly round and do not vary in shape or size. Exceptions are teeth located on both extremes of the posterior margin, which are very small, and the jaw battery includes three distinctively larger teeth, which are centrally aligned at the posterior margin.

Remarks. Both MPC-456 and MPC-627 are assigned to the family Labridae because of being a highly ossified triangular pharyngeal tooth plate densely covered by molariform-like teeth. The "morphotype 1" (MPC-627) differs from *Labrodon* sp. by having posteromedial molar-like teeth that are larger, globular, and trapezoid to rectangular in shape, overlapping each other. The "morphotype 2" (MPC-456) differs from *Labrodon* sp. because it is densely covered with very small molariform-like teeth.

The family Labridae is currently represented by 71 genera and 557 species occurring in all oceans (Froese & Pauly, 2020). The fossil record of this family extends back into the Eocene (Bannikov & Carnevale, 2009). Neogene records are very abundant in North America (*e.g.*, Barnes *et al.*, 1981; Purdy *et al.*, 2001) and Europe (*e.g.*, Carnevale, 2015) but almost absent from New Zealand (Schwarzhans, 2019). In South America, the family was reported from the middle–late Miocene of Argentina (Cione *et al.*, 2000), and late Miocene of Chile (Walsh, 2001; Suárez & Marquardt, 2003; Suárez *et al.*, 2003).

Order PERCIFORMES Bleeker, 1859
Family HAEMULIDAE Gill, 1885
Subfamily HAEMULINAE Gill, 1885

Genus ***Anisotremus*** Gill, 1861

Type species. *Sparus virginicus* Linnaeus, 1758: 281.

Anisotremus sp.
Figure 5.1

Referred material. One left ceratobranchial from the lower pharyngeal jaw battery (MPC-744).

Geographic occurrence. Norte Bahía Caldera, Chile.

Description. The left ceratobranchial is irregular triangular and measures about 7 cm in length. It has a lateral process positioned in the middle part of the outer margin. In ventral view, it is almost flat, and it is slender in lateral view. It is covered dorsally by large rounded to oval alveoli indicating the presence of massive molariform-like teeth. Larger alveoli are arranged in three main lines, distally decreasing in size anteriorly at the base of the horn.

Remarks. This specimen is assigned to *Anisotremus* because of its triangular shape with large rounded to oval alveoli and an elongated anterior horn-shaped process and lateral process placed in the middle part of the outer margin. The specimen described here is similar to the equivalent element in *Anisotremus surinamensis* because of the well-developed molariform-like teeth cover the ceratobranchial.

The genus *Anisotremus* is represented by eight extant species distributed in the eastern Pacific and western Atlantic oceans (Froese & Pauly, 2020). Specimens of *Anisotremus* are very rare in the fossil record, being reported only from the Pliocene of the United States (Fitch & Lavenberg, 1983) and the Holocene of Turks and Caicos Islands (O'Day, 2002).

Order ACANTHURIFORMES Jordan, 1923
Suborder SCIAENOIDEI Betancur-R. *et al.*, 2013
Family SCIAENIDAE Cuvier, 1829
Sciaenidae gen. *et* sp. indeterminate
Figure 5.2–5.4

Referred material. A single, fragmentary left maxilla (MPC-751).

Geographic occurrence. Norte Bahía Caldera, Chile.

Description. MPC-751 is a left, fragmentary maxilla, preserving only its anterior portion (Fig. 5.2–5.4). It is robust and comprises a distinct head and shaft. The proximal epiphysis is a composite condyloid joint for articulation with the premaxilla and the vomer. The anterior part of the joint has a thickened edge and two concavities close to the processes (Fig. 5.3). The lateral process is broken, and corresponding characters are not visible. The internal process is globular, thickened, and displays a shallow, concave depression. In lateral view, a concave indentation is also present in the region of the external process (Fig. 5.3).

Remarks. The maxillary of members of the family Sciaenidae is very diagnostic and comprises a distinct head and shaft (Fig. 5.3–5.4). Ventrally it has two condyles to articulate with the premaxillary process, and posterodorsally, it has an articulation with the anterior process of the palatine (Sasaki, 1989).

The family Sciaenidae is currently represented by 67 genera and 286 globally distributed species (Froese & Pauly, 2020). The fossil record of this family extends back into the late Cretaceous (Grandstaff *et al.*, 1992). Neogene records are abundant in North America (Gillette, 1984; Emslie & Morgan, 1994; González-Castillo *et al.*, 2020), Europe (Bannikov *et al.*, 2018), and tropical America (Aguilera *et al.*, 2016; González-Castillo *et al.*, 2020). In the eastern Pacific of South America, the family was reported from Ecuador (Carnevale *et al.*, 2011) and Chile (Suárez *et al.*, 2010; Carrillo-Briceño, 2011). The specimen described here thus confirms the presence of sciaenid fishes in the Miocene of Chile.

Subfamily STELLIFERINAE Sasaki, 1989

Stelliferinae gen. *et* sp. indeterminate
Figure 5.5–5.7

Referred material. An occipital portion of a cranium (MPC-732).

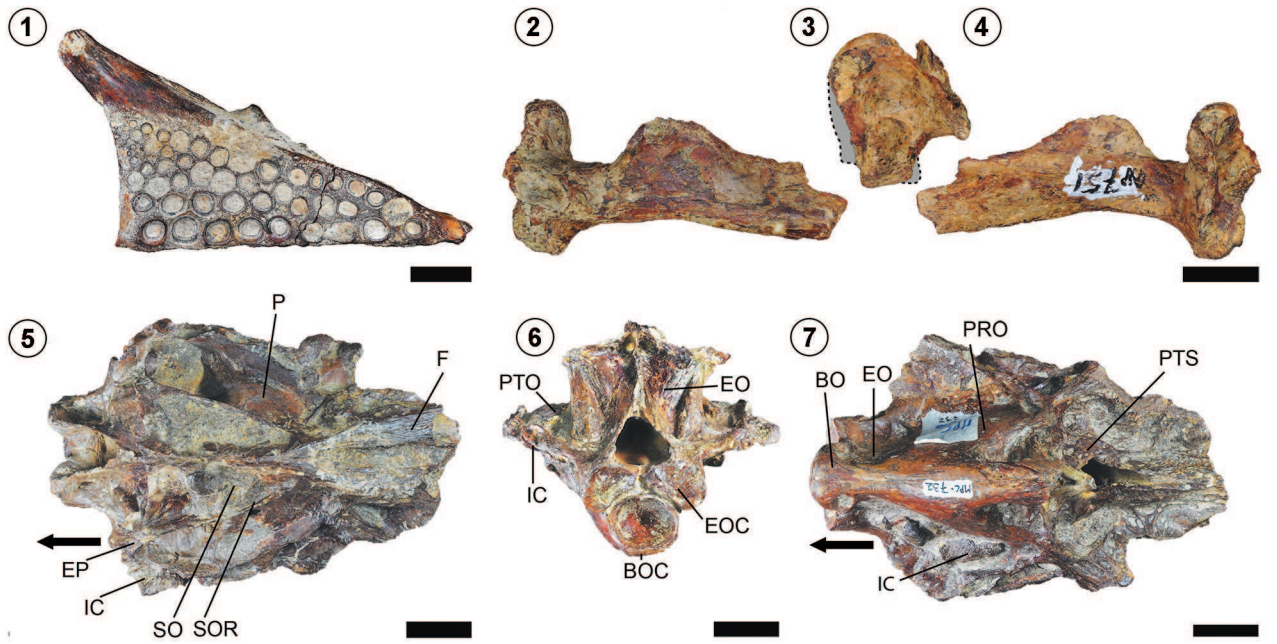

Figure 5. 1, ***Anisotremus*** sp., MPC-744; one left ceratobranchial from a lower pharyngeal jaw battery. **2–4,** Sciaenidae gen. *et* sp. indeterminate, MPC-751; anterior part of the left maxilla. **5–7,** Stelliferinae gen. *et* sp. indeterminate, MPC-732; an occipital region of a cranium. Scale bars **1, 5–7,** 1 cm; **2–4,** 2 cm.

Geographic occurrence. Norte Bahía Caldera, Chile.

Description. MPC-732 preserves parts of the cranium and is 112 mm in length, 57 mm in width, and 58 mm in height (Fig. 5.5–5.7). The anterior section of the cranium is not preserved. Nasals, the vomer, the ethmoid, the lateral ethmoids, and the parasphenoid thus are lacking. The supraoccipital, parietal, and pterotic bones contact the frontals posteriorly, whereas the sphenotic and pterosphenoid contact the frontals posteroventrally. The frontals are ornamented dorsally with low, antero-posteriorly directed ridges. The frontals and pterotics are highly cavernous. The supraoccipital has a fracture in its suture region that evidences a dorsal crest in the cranium. The intercalars are in wide contact with the exoccipitals. The exoccipital condyles are separated from each other. The prootic constitutes the posteroventral wall of the orbit and the wall of the auditory bulla. The auditory bulla is large, indicating the presence of big size otoliths and notched.

Remarks. MPC-732 is assigned to the subfamily Stelliferinae based on two cranial characters: notched auditory bulla and exoccipital condyles not broadly joined to each other (Sasaki, 1989). According to Sasaki (1989), these two traits represent autapomorphies of his group II that includes only one subfamily, Stelliferinae represented by six extant (Sasaki, 1989) and two extinct genera (Aguilera *et al.*, 2016). The extant representatives are currently distributed in tropical and subtropical environments of the eastern Pacific and western Atlantic oceans (Froese & Pauly, 2020). Neogene fossils of this subfamily are very abundant in Brazil, Costa Rica, Ecuador, Panama, Trinidad, and Venezuela (Aguilera *et al.*, 2011, 2016). The specimen described here represents the first fossil record of the Stelliferinae from the eastern Pacific of South America.

DISCUSSION AND CONCLUSIONS

Fish paleodiversity and paleobiogeographic significance

Here we present a compendium of the published and unpublished fish fauna from the Bahía Inglesa Fm. (Tab. 1). The overall bony fish paleodiversity of the Bahía Inglesa Fm. includes at least 21 recognized taxa (Tab. 1), being one of the most diverse Neogene assemblages along the southeastern Pacific (**SEP**). At least eight taxa represented by four families, one subfamily, seven genera, and one species correspond to the newly reported bony fish paleodiversity from the Bahía Inglesa Fm. here (Tab. 1). Of these, *Sardinops* cf. *sagax* is reported for the first time in the fossil record of Chile (Table 1). *Labrodon* sp., *Sarda* sp., and Stelliferinae indet., are reported for the first time in the SEP. *Anisotremus* sp. and *Semicossyphus* sp. are reported for the first time in the Southern Hemisphere, while *Gymnosarda* sp. is reported for the first time from Neogene deposits.

From a paleobiogeographic point of view, *Labrodon* is an extinct taxon, *Gymnosarda* became regionally extirpated from the SEP, and *Anisotremus*, *Genypterus*, *Makaira*, *Sarda*, *Sardinops*, and *Semicossyphus* still have extant representatives in the region (Tab. 2). The high percentage of persistent taxa seems similar to that observed in chondrichthyans, which shows low extinction rates (3%) in the temperate SEP during the Neogene–Quaternary transition (Villafaña & Rivadeneira, 2014). From the reported fossil assemblage, five out of six taxa remained in the SEP (*Genypterus*, *Makaira*, *Sarda*, *Sardinops*, and *Semicossyphus*) with a wider southern latitudinal range, whereas *Anisotremus* is characterized by a decrease in its southern latitudinal range. Most of the fossil taxa reported here with an increment in their latitudinal range are present nowadays in southern Chile (>40° S) with at least one species (Tab. 2). For example, the Peruvian grunt (*A. scapularis*) is the only species of the genus *Anisotremus* occurring in Chile today (Froese & Pauly, 2020), demonstrating that the southern latitudinal range for this species is smaller today than in the past. On a local scale (ca. 27–29° S), there are no significant changes in the composition of families since most of them have living representatives in the same region (Tab. 2). At the genus level, *Gymnosarda* is absent today in the study region (Tab. 2). This could suggest a low compositional replacement of fishes both on family and genus levels from the Neogene to today. Despite these results, perspectives might change as more fossil taxa from the region are recovered and described.

The composition similarity analysis shows that the Bahía Inglesa Fm. shares low family-level similarities with the faunas of the Pisco Fm. in Peru (Sørensen-Dice similarity index, SD= 0.2; shared taxa: Scombridae and Xiphiidae), and the Horcón Fm. in Central Chile (SD= 0.36; shared taxa: Merluciidae, Ophidiidae, Sciaenidae, and Xiphiidae). The genus-level comparison is suitable for now only with the faunas from the Horcón Fm. because the fossil fishes from other geological units are only identified at the family level

TABLE 1. Record of bony fish taxa in Neogene units of the temperate Pacific of South America.

Fossil taxa	Pisco	La Portada	Bahía Inglesa	Coquimbo	Horcón	Navidad	Ranquil	Reference
Acanthocybium sp.	-	-	1	-	-	-	-	4
aff. ***Psamoperca*** sp.	1	-	-	-	-	-	-	1, 7
Alosinae indet.	1	-	-	-	-	-	-	1
Aplodactylus sp.	-	-	-	-	1	-	-	10
Bovichtus sp.	-	-	-	-	1	-	-	10
cf. ***Anisostremus*** sp.	-	-	1	-	-	-	-	11
cf. Ariidae indet.	1	-	-	-	-	-	-	1, 7
cf. ***Xiphiorhynchus*** sp.	1	-	-	-	-	-	-	1
Cheilodactylus sp.	-	-	-	-	1	-	-	10
Cilus gilberti	-	-	1	-	-	-	-	9
Eleginops sp.	-	-	-	-	1	-	-	10
Cybiidae indet.	1	-	-	-	-	-	-	1
Sicyases sp.	-	-	-	-	1	-	-	10
Girella sp.	-	-	-	-	1	-	-	10
Merlucciidae indet.	-	-	-	-	1	-	-	10
Gymnosarda sp.	-	-	1	-	-	-	-	11
Genypterus sp.	-	-	1	-	1	-	-	10,11
Hypoplectrodes sp.	-	-	-	-	-	-	1	12
Istiophoridae indet.	-	-	1	-	-	-	-	3, 11
Labridae indet.	-	1	1	-	-	-	-	3, 5, 6, 11
Labrodon sp.	-	-	1	-	-	-	-	11
Makaira sp.	-	-	1	-	-	-	-	8, 11
Hippoglossina sp.	-	-	-	-	1	-	-	10
Merluccius gayi	-	-	1	-	-	-	-	9
Oplegnathidae indet.	-	-	1	-	-	-	-	4
Pomacentridae indet.	1	-	-	-	-	-	-	1
Sarda *sp.*	-	-	1	-	-	-	-	11
Sardinops aff. ***S. sagax***	-	-	1	-	-	-	-	11
Sciaenidae indet.	-	-	1	-	-	-	-	11
Scombriformes indet.	-	-	1	-	-	-	-	11
Scombridae indet.	1	-	1	1	-	-	-	1, 2, 3, 4, 11
Semicossyphus sp.	-	-	1	-	-	-	-	11
Serranidae indet.	-	-	1	-	-	-	-	2
Cilus sp.	-	-	-	-	1	-	-	10
Sphyraenidae indet.	1	-	-	-	-	-	-	1
Steindachneria svennielseni	-	-	-	-	-	1	-	13
Stelliferinae indet.	-	-	1	-	-	-	-	11
Tetraodontiformes indet.	1	-	-	-	-	-	-	1
Thunnus sp.	-	-	1	-	-	-	-	2
Triglidae indet.	1	-	-	-	-	-	-	1, 7
Xiphias gladius	-	-	1	-	-	-	-	4
Xiphiidae indet.	1	-	-	-	1	-	-	1, 10
Total	11	1	21	1	11	1	1	

References: 1, de Muizon & DeVries (1985); 2, Long (1993); 3, Walsh (2001); 4, Suárez *et al.* (2002); 5, Suárez *et al.* (2003); 6, Suárez & Marquardt (2003); 7, Báez (2006); 8, Gutstein *et al.* (2008); 9, Suárez *et al.* (2010); 10, Carrillo-Briceño (2011); 11, this study; 12, Pérez (2017); 13, Nolf (2002).

(de Muizon & DeVries, 1985; Long, 1993). According to our results, the Horcón Fm. displays a low similarity value (SD= 0.09; shared taxa: *Genypterus*). The results of our comparative analysis suggest that the fish assemblages from Bahía Inglesa and Pisco formations may belong to different paleobiogeographic provinces during the late Miocene (Tab. 1). This could be explained by the differences in the oceanographic regimes along the Chilean and Peruvian coast in the past (see DeVries & Frassinetti, 2003).

The low similarity value between the Bahía Inglesa and Horcón formations could also be related to a faunal turnover that occurred in the region at the Miocene–Pliocene transition (J. D. Carrillo-Briceño, personal communication, May 10, 2021), or other paleoenvironmental changes (Partarrieu *et al.*, 2018), probably triggered by a global temperature decrease (Miller *et al.*, 2020). Nevertheless, taphonomic and sampling differences could be strong influencing factors as well. Further detailed paleontological analyses of fish assemblages are much needed at most locations along the SEP to fully understand the paleobiogeographic structure and dynamics of marine fishes during the Neogene in South America.

Paleoenvironmental reconstruction

Different authors, using multiple proxies, have proposed paleoenvironmental reconstructions for the Bahía Inglesa Fm. (*e.g.*, Marquardt, 1999; Walsh & Hume, 2001; Achurra *et al.*, 2009; Henríquez, 2006; Walsh & Suárez, 2006). Benthic foraminifera has produced depth range estimates from the littoral zone to the upper continental slope at about 50–500 m depth (Marchant *et al.*, 2000) and 800 m (Henríquez, 2006). The combined presence of seabird remains together with chondrichthyans indicates shoreline to sublittoral environments with depths less than 200 m (Walsh & Hume, 2001; Walsh & Suárez, 2006). Studies of the sedimentary facies indicate a sublittoral to neritic environment up to 500 m (Marquardt, 1999). Petrographic and geochemistry analyses of manganese nodules show that these were deposited on the upper continental slope (200–2,564 m) by debris

TABLE 2. Biogeographic distribution of Neogene fish taxa described in this study. Examples of species currently distributed in Chile are included.

Family	Fossil taxa	Global status	Biogeographic dynamic	Climatic zone	Habitat	Extant species in Chile	Southern Latitude Chile	References
Alosinae	***Sardinops*** aff. ***S. sagax***	Living	Increased	Tr-St-T	P-N	***S. sagax***	-44	1
Haemulidae	***Anisotremus*** sp.	Living	Decreased	Tr-St-T	D-Re	***A. scapularis***	-23	1
Istiophoridae	Istiophoridae indet.	Living	Increased	Tr-St-T	P-O	***M. nigricans***	-40	1
Istiophoridae	***Makaira*** sp.	Living	Increased	Tr-St-T	P-O	***M. nigricans***	-40	1
Labridae	Labridae indet.	Living	Increased	Tr-St-T-P	D-Re-P-N	***S. darwini***	-33	1
Labridae	***Labrodon*** sp.	Extinct	Globally extinct	-	-	-	-	-
Labridae	***Semicossyphus*** sp.	Living	Increased	Tr-St-T	Re-D	***S. darwini***	-37	4
Ophidiidae	***Genypterus*** sp.	Living	Increased	Tr-St-T	Bd-D	***G. blacodes, G. chilensis***	-55	1, 3
Sciaenidae	Sciaenidae indet.	Living	Increased	Tr-St-T	D-Re-P-N	***C. gilberti***	-37	1
Sciaenidae	Stelliferinae indet.	Living	Regionally extinct	Tr-St	D-Re-P-N	absent	-	1
Scombridae	***Gymnosarda*** sp.	Living	Regionally extinct	Tr-St-T	P-Re	absent	-	1
Scombridae	***Sarda*** sp.	Living	Increased	Tr-St-T	P-N	***S. chilensis***	-41	2
Scombridae	Scombridae indet.	Living	Increased	Tr-St-T	P-O-N-Re	***S. chilensis***	-41	1

Climatic zones: **Tr,** Tropical; **St,** Subtropical; **T,** Temperate; **P,** Polar. Habitat: **Bd,** Bathydemersal; **D,** Demersal; **P,** Pelagic; **N,** Neritic; **O,** Oceanic; **Re,** Rocky environment. References: 1, Froese & Pauly (2020); 2, Collette (1995); 3, Vega *et al.* (2015); 4, Chirichigno (1998).

flows and turbidity currents associated with a submarine paleocanyon (Achurra *et al.*, 2009; Le Roux *et al.*, 2016). A recent detailed study of the facies of the Bahía Inglesa Fm. shows that the depositional environment experienced an overall uplift-subsidence-uplift pattern (Le Roux *et al.*, 2016). Consequently, the different depth interpretations for this geological unit likely are related to this subsidence pattern (see Le Roux *et al.*, 2016), with slow sedimentation rates and by the lateral changes of the facies to shallower conditions.

Our paleobathymetric analysis includes all previously and the newly reported fishes from the Bahía Inglesa Fm. (Fig. 6). Although published bony fish and chondrichthyan records from this unit lacks detailed stratigraphic information, these fishes have been reported in the Cerro Ballena (8.4 Ma), Mina Fosforita (7.0 Ma.), and Quebrada Blanca members (2.4 Ma) (Long, 1993; Suárez & Marquart, 2003; Gutstein *et al.*, 2008; Suárez *et al.*, 2010; Pyenson *et al.*, 2014; Villafaña & Rivadeneira, 2018; Villafaña *et al.*, 2019). We consider that the results of our paleobathymetric analysis could be a good estimator for the Mina Fosforita Member because most of the published material comes from Caldera (Long, 1993; Villafaña & Rivadeneira, 2018). Despite the degree of uncertainty of the locality for some records, we decided to include all available data because most of them are associated with the phosphatic bonebed and the sands and siltstones layers of the Mina Fosforita Member, which has an age of ~7.0 Ma (Marquardt, 1999; Canto *et al.*, 2008; Le Roux *et al.*, 2016). The paleobathymetric analysis shows that the Mina Fosforita Member likely ranged from 200–300 m depth, which is supported by the overlapping depth range of 39 taxa representing 66.1% of the total analyzed taxa (Fig. 6). The depth estimated by the weighted paleobathymetric analysis for 10,000 replicated samples range was 99 to 382 m within the 95% confidence interval with a median depth of 253 m (Fig. 6). This estimate corresponds to a depositional environment ranging from the middle shelf (outer neritic) to the upper bathyal environment (suboceanic) with a mean depth in an upper bathyal environment (Fig. 6). Our paleobathymetric estimation is consistent with a geohistorical depth estimation (Hardenbol *et al.*, 1998) for Caldera that shows a submarine canyon deposited in the Chorrillos member ca. 7.5 Ma, which is related to a topographic outlier of the JFR as can be seen along the present ridge of Chile coast (Le Roux *et al.*, 2016). The habitat preferences that characterize the modern representatives of the fish genera reported here show that the fish fauna of the Mina Fosforita Member is distributed in three types of available habitats (Tab. 2). The first habitat is pelagic, represented by members of the families Clupeidae (*Sardinops* sp. cf. *S. sagax*), Istiophoridae (*Makaira* sp.), Xiphiidae (*Xiphias* sp.), and Scombridae (*Sarda* sp. and *Acanthocybium* sp.) (Boyce *et al.*, 2008; Pepperell & Harvey, 2010; Shimose *et al.*, 2010). The second habitat is bathydemersal, represented by members of Labridae (*Semicossyphus* sp.) and Haemulidae (*Anisotremus* sp.), taxa typically inhabiting shallow-water rocky environments (Froese & Pauly, 2020). About the third habitat, it could be referred to as benthic, being represented by the family Ophidiidae (*Genypterus* sp.), of which extant species prefer rocky bottoms on the continental shelf (Nielsen *et al.*, 1999). The relative abundance and better preservation of pelagic and bathydemersal fossil fishes like *Sardinops* and Istiophoridae and chondrichthyans like *Callorhynchus* sp., *Odontaspis ferox*, *Hexanchus* sp., *Pristiophorus* sp., and *Squatina* sp., support the preliminary estimated mean depth and the pelagic environment (Fig. 6) (Froese & Pauly, 2020).

The cranial material in our sample belongs to fishes with a durophagous feeding strategy (*e.g.*, *Labrodon* sp., *Anisotremus* sp., *Sciaenidae*) is represented by pharyngeal jaws that are worn on the surfaces, thus suggesting active transport. However, some specimens with little wear can be explained by lateral facies change towards a shallower environment (Fig. 4.5–4.12). For example, transported macrofossils into deeper water by storm events were reported for the Bahía Inglesa Fm. (Le Roux *et al.*, 2016). The hypothesis of reworked material agrees well with the presence of type P and D phosphates in the Mina Fosforita Member, where the formers are commonly transported to the latter due to cementation with carbonate fluorapatite, forming hardground nodules during upwelling of cold, deep ocean waters rich in phosphate and other nutrients (Le Roux *et al.*, 2016). The presence of phosphate minerals and calcareous fossil bones in some horizons and the proliferation of plankton in the Bahía Inglesa Fm. could be only explained by a strong upwelling system (Achurra *et al.*, 2009; Pyenson *et al.*, 2014). *Sardinops* is the most abundant taxon according to field campaigns that currently are in progress (Oyanadel-Urbina,

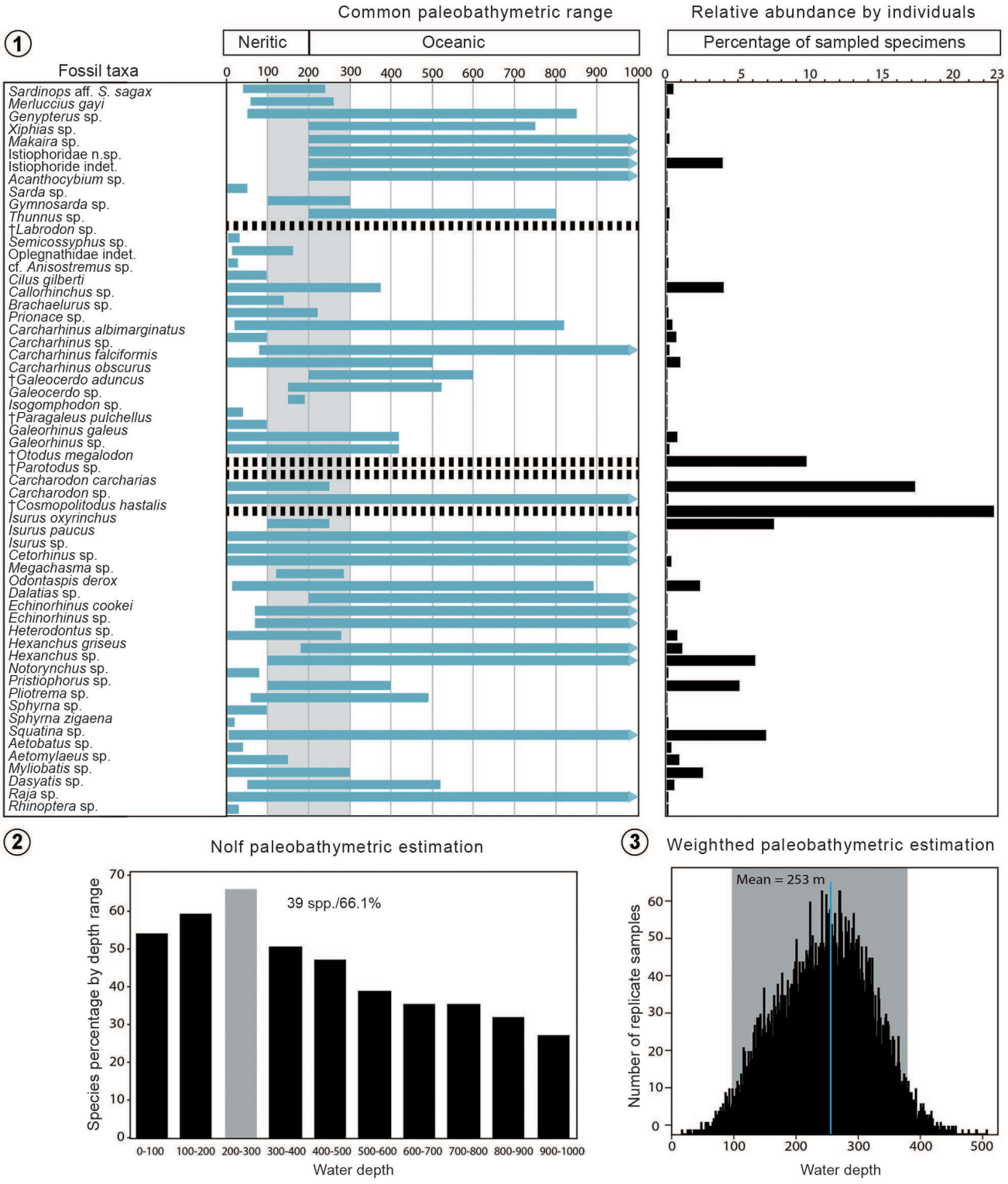

Figure 6. Paleobathymetric estimation for the Bahía Inglesa Fm. using all available fish taxa, their relative abundance and diversity. **1,** Solid lines indicate the common paleobathymetric range for each taxon, arrows indicate that the bathymetric range is greater, a dashed black line indicates that there is no information for the taxon and it was removed from the analysis. The gray shadow indicates the 95% confidence interval for the most probable depth range for this assemblage; **2,** For the Nolf technique, 66.1% of the studied taxa are represented in a depth range of 200–300 m; **3,** The weighted paleobathymetric estimation indicates a mean of 252.83 m after resampling with 10,000 simulations.

pers. observ.), and extant representatives are good indicators of upwellings in modern environments (Bowen & Grant, 1997; Espinoza *et al.*, 2009; Van der Lingen *et al.*, 2001; Kreiner *et al.*, 2001).

The Late Miocene fish assemblage from Bahía Inglesa seems to be associated with warmer water conditions than those today in Chile (Fig. 6). This result agrees with the presence of some fossil chondrichthyans (Walsh, 2001; Villafaña & Rivadeneira, 2018; Villafaña *et al.*, 2019), marine mammals (De Los Arcos *et al.*, 2017), mollusks (Ibaraki, 1992; DeVries & Frassinetti, 2003), and planktonic foraminifera (Tsuchi, 1992; Ibaraki, 2001), that are indicators of a warming period during the deposition of the sediments of the Bahía Inglesa Fm. during the late Miocene (Ibaraki, 1992; Tsuchi, 1992; Ibaraki, 2001; DeVries & Frassinetti 2003; Oerter *et al.*, 2016), before the Pliocene-Pleistocene cooling (Martínez-Pardo, 1990; Tsuchi 1992; Le Roux, 2012). The abundance of billfishes and scombrids is a nonlinear function of water temperature and the peak of species occurrences to have an optimal thermal range of 21–24°C (Fierstine, 1978, 1990; Nakamura, 1983; Boyce *et al.*, 2008). Extant marlins, sailfishes, and most small tropical tuna species possess a higher tolerance for warmer waters and lower tolerance for colder waters (Boyce *et al.*, 2008). The proposed preferences to warmer environments are in accordance with warming episodes during the late Miocene in the SEP (Martínez-Pardo, 1990; Tsuchi, 1992; DeVries & Frassinetti, 2003; Le Roux, 2012) and are consistent with the current distribution of extant species of *Sarda*, which are found in tropical, subtropical and temperate waters between 12 and 27 °C (Collete & Nauen, 1983).

Perspectives

We report here 21 bony fish taxa from Bahía Inglesa Fm. of which one represents the first fossil record for Chile, two new records for the SEP, one first record for South America, two new records for the Southern Hemisphere, and one first record for the Neogene. To date, this work represents the most detailed effort to reconstruct the taxonomic diversity, paleoenvironment, and paleogeographic relationships of the fossil fishes from the Bahía Inglesa Fm. Our analyses indicate that the Bahía Inglesa Fm. harbors the most diverse fish fauna currently known from the Miocene of Chile. The paleoenvironmental reconstruction supports the hypothesis that the Bahía Inglesa localities studied here likely were deposited in an uppermost bathyal (suboceanic to oceanic) environment. Due to our limitations and insufficient knowledge, future studies should focus on collecting in situ material with detailed and new stratigraphic information in order to unambiguously establish the stratigraphic ranges and to improve the taxonomic resolution of the fossil findings in Chile. This work represents only a small fraction of the true fossiliferous potential of the Bahía Inglesa Fm., and so, further paleoichthyological research will likely improve our understanding of the Neogene SEP fish assemblages.

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